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Conservatism in the karyotypes of two African Mole rats (Rodentia, Bathyergidae)

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Abstract

Investigated the chromosomes and G band patterns of two genera of the African rodent family Bathyergidae. *Heterocephalus glaber* and *Heliophobius argenteocinereus* have a diploid number of 60, similar karyotypes and similar G band patterns. The karyotypes are compared with those of other fossorial rodents. It is concluded that fossorial rodents fall into two categories: those with conservative karyotypes like Bathyergidae and Octodontidae and those with variable karyotypes like Geomyidae, Spalacidae and Ctenomyidae.

The difference between the two categories does not seem to depend on the social structure of the two groups. Fossorial rodents, therefore, do not necessarily have different evolutionary potential or karyotype variability from other rodents just because of their underground way of life.

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Introduction

MATTHEY (1956) studied the chromosomes of several unrelated fossorial rodents looking for similarities which he did not find. Recently, it has been generally assumed that the karyotypes of fossorial rodents exhibit greater diversity both between species and within species than those of most other rodents (BUSH et al. 1977).

The karyotypes of two genera of Bathyergidae are reported here and the characteristics of fossorial rodent karyotypes discussed.

MATTHEY reported 54 mainly metacentric and submetacentric chromosomes in the symmetrical karyotype of the South African bathyergid *Georychus capensis*. Neither *Bathyergus* nor *Cryptomys* karyotypes are known.

Materials and methods

The bathyergids were obtained during a two month stay at the University of Nairobi.

Heterocephalus glaber, the naked mole rat or sand puppy, came from Mtito Andei in southern Kenya. Three males and two females were used in these studies.

The grey mole rat or silver blesmol, *Heliophobius argenteocinereus*, inhabits extensive tunnel systems in the black cotton soil of the Athi Hills south east of Nairobi where it thows up easily recognisable piles of soil. Trapping failed to catch any *Heliophobius* and it took ten days of digging to get three animals. All were females.

The identity of the species was checked against specimens in the British Museum (Natural History) in London.

The animals were killed with chloroform. Blood samples of between 0.5 and 1.0 ml were taken from the heart and cultured for karyotype study by the technique of HUNGERFORD (1965).

Bone marrow preparations were made from *Heliophobius* by a modification of the blood culture technique. The marrow was flushed from the femur with a drop of heparin into Difco TC chromosome culture medium and left for 24 hours at room temperature (about 23 °C). The culture was transferred to 37 °C for five hours. The cells were prepared in the same way as the blood leucocytes.

Preparations were also made from the testes of the three male *Heterocephalus*. The technique was essentially that of EVANS et al. (1964) and MEREDITH (1969) with the addition of a few drops of vinblastine sulphate to the hypotonic sodium citrate solution. The preparations were divided into three and left for 10, 15 and 20 minutes in hypotonic solution before fixing. The longest time was the best. 45% acetic acid was added in the final stages to assist spreading on the slide. The meiotic metaphases proved useful for an initial count of the haploid chromosome number as the diploid number is high and many of the chromosomes small. Some specimens from one individual of each genus were G-banded by the trypsin digestion method and Giemsa staining of SEABRIGHT (1972).

Results

Heterocephalus glaber

Mitotic plates from five animals, three males and two females and meiotic plates from the males were counted. Ten mitotic plates of each animal were karyotyped and arm ratios measured. Ten meiotic plates from each male were photographed for counting chiasmata.

The diploid number of *Heterocephalus glaber* is 2n = 60 (Fig. 1).

The chromosomes grade from chromosome 1 which is medium in length (5.7% of the haploid female set) to chromosomes 25 to 29 which are microchromosomes (less than 2%). Chromosome 29, at 1% of the set is conspicuously smaller than any of the others. The majority of the chromosomes are metacentric or submetacentric with short arm to long arm ratios between 1 : 1 and 1 : 3. Chromosomes 5, 8, 9, 12, 13, 14, 18 and 23 are small subacrocentrics with arm ratios between 1 : 3 and 1 : 7.

The X chromosome is metacentric and, at 5.5% of the haploid set, the second longest chromosome and a standard mammal X chromosome (OHNO et al. 1964).

The Y chromosome is a metacentric very small microchromosome, 0.9%.

The NF (subacrocentrics count as two-armed) is 120.

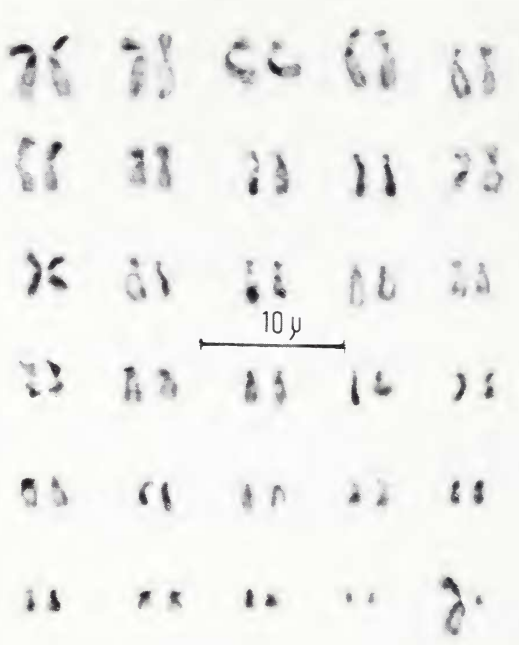

Fig. 1. Giemsa banded karyotype of male *Heterocephalus glaber*

The karyotype is symmetrical and without distinguishing features except for the small size of chromosome 29.

Meiotic plates show many chromosomes with two or three chiasmata so that the mean number of chiasmata per chromosome is 1.8 (Fig. 2) and the recombination index 81.

The G-banded preparations show few readily identifiable features but they provide a basis for the comparison of individual chromosomes with those of *Heliophobius*. The main banding feature is the absence of dark bands in the centromeric regions. The X chromosome has two dark bands in the short arm and three in the long arm. This pattern is more like that of some other African 'hystricomorphs' (George 1979) and the South American Ctenomyidae than that found in murids (Committee for a Standardised Karyotype of *Rattus*

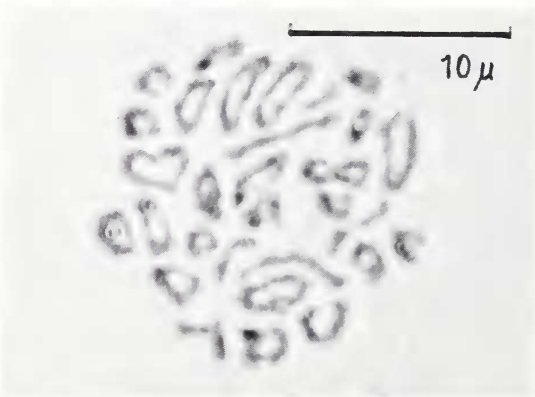

Fig. 2. Meiotic plate from a testis preparation of *Heterocephalus glaber*

norvegicus, 1973) cricetids (Committee for Standardisation of Chromosomes of *Peromyscus,* 1977) or sciurids (NADLER et al. 1975).

Chromosome 1 has two wide bands in the short arm, a pale centromeric region and one wide and two narrow dark bands in the long arm.

Heliophobius argenteocinereus

Mitotic plates from bone marrow preparations of three females were counted and ten from each individual karyotyped.

The diploid number of *Heliophobius argenteocinereus* is 2n = 60 (Fig. 3).

The karyotype is symmetrical and the chromosomes resemble closely those of *Heterocephalus glaber,* grading from the medium chromosome 1 to the microchromosome 29.

The majority of the chromosomes are metacentric or submetacentric with three small subacrocentrics: chromosomes 13, 18 and 23. The most conspicuous feature of the set is chromosome 9 which is acrocentric. Chromosome 29, at 1.9% of the haploid set, is almost twice as long as the *Heterocephalus* chromosome 29 and not strikingly shorter than chromosome 28.

The X chromosome is assumed to be the metacentric second longest of the set. This assumption was made because it is the same size and shape as the X chromosome of *Heterocephalus* and has the same pattern of G bands. The Y chromosome is not known.

The NF is 118. No meiotic plates were available.

The G-banded mitotic plates, like those of *Heterocephalus*, show few outstanding fea-

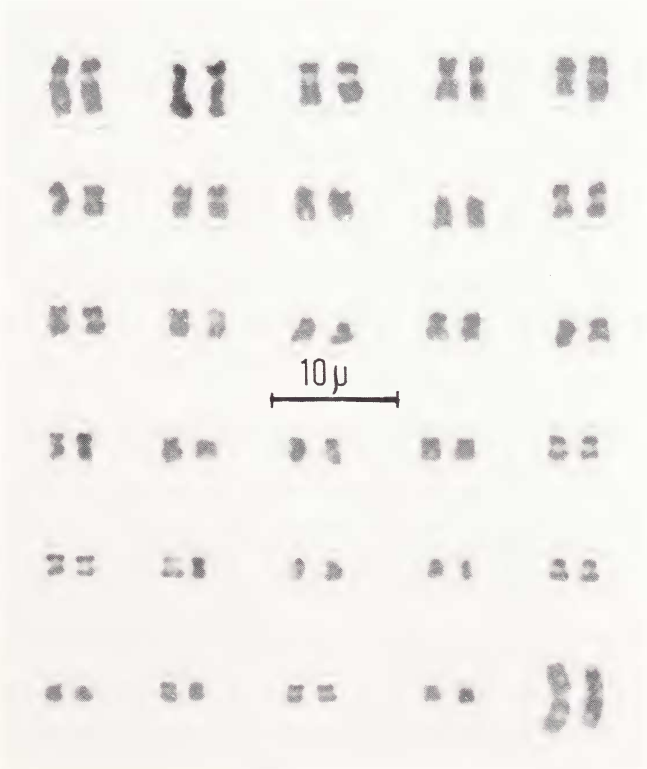

Fig. 3. Giemsa banded karyotype of female *Heliophobius argenteocinereus*

tures. Some 67% of the chromosomes can be equated with those of *Heterocephalus* and the majority of the remainder differ probably because the *Heterocephalus* chromosomes were more stretched during preparation and show their pattern more clearly. The distinguishing features of the karyotypes, the subacrocentrics, the near subacrocentrics and the very small chromosomes, all have similar band patterns to those of *Heterocephalus*. The single arm of *Heliophobius* chromosome 9 has the same bands as the long arm of *Heterocephalus* chromosome 9. It is, however, impossible to determine where the short arm of the *Heterocephalus* chromosome is represented. The pattern of chromosome 4 and 14 is different from *Heterocephalus*. Chromosome 14 is metacentric in *Heliophobius* and subacrocentric in *Heterocephalus*. In both genera the chromosome has three dark bands but they are all in the long arm of *Heterocephalus* chromosome 14 and in *Heliophobius* chromosome 14 one dark band is in the short arm and the other two in the long arm. This may represent a pericentric inversion difference. Chromosome 4 appears to have two dark bands in the short arm and three narrow dark bands in the long arm in *Heterocephalus* but only one dark band in the short arm and two wide dark bands in the long arm in *Heliophobius*.

Discussion

The striking similarity between the karyotypes of the fossorial *Heterocephalus glaber* and *Heliophobius argenteocinereus* is unexpected. The specimens were taken from randomly available populations 200 km apart in Kenya and yet the karyotypes are so similar as to represent hardly more than the equivalent of a local variation in many other fossorial rodents. Only chromosomes 4, 14, 9 and 29 conspicuously differentiate the two genera. There may be a few small banding differences in other chromosomes but they were difficult to assess.

Georychus capensis was reported to have 2 n = 54 (Matthey 1956) with mainly metacentric and submetacentric chromosomes and, therefore, a high NF though neither as high nor identical with those of its relatives reported here. Matthey also reported a comparatively long Y chromosome which was not found in *Heterocephalus*. The details of the *Georychus* karyotype are not sufficiently clear for a useful comparison to be made with the other two genera.

The surprising conservatism of karyotype in only distantly related fossorial genera has also been found in the octodontid *Spalacopus cyanus* of Central Chile. Reig et al. (1972) studied the karyotypes of five populations, some separated by over 100 km. The karyotypes were identical except for one individual which had a dimorphic pair of chromosomes. Furthermore, the karyotype of *Spalacopus cyanus* is almost identical with that of its near relative, the non-fossorial degu *Octodon degus* (Fernandez 1968), differing only in the length of chromosome 1 and the Y chromosome.

Like *Heterocephalus* and *Heliophobius, Octodon* and *Spalacopus* are morphologically distinct.

These two sets of mole rats form a marked contrast to the Geomyidae, the Spalacidae and Ctenomyidae which, characteristically, show variations in their karyotypes. Populations of the spalacid *Spalax ehrenbergi* grade from 2n = 52 at the northern end of the range, in Lebanon, to 2n = 60 in the Negev and Egypt (Wahrman et al. 1969; Lay and Nadler 1972). Species of *Ctenomys* ranging from Peru to Tierra del Fuego, have diploid numbers from 26 to 68 and equally varied NFs (Kiblisky and Reig 1966; Reig and Kiblisky 1969). Among the Geomyidae, *Thomomys talpoides* shows considerable variation, 2n = 40 to 60 and NF = 70 to 82 (Thaeler 1968, 1974; Berry and Baker 1971) with a geographical gradient; *Geomys* species range from a supposed basic 2n = 72 to 2n = 38 (Baker 1971; Selander et al. 1974; Williams and Genoways 1975) and *Pappageomys* ranges from 2n = 46 to 2n = 40 with geographical variation of chromosome number within one of the species, *P. castanaps* (Berry and Baker 1972). There is less to be said about the Rhizomyidae where the African

Tachyoryctes splendens has 2n = 48 (MATTHEY 1956) and the Asian *Rhizomys sumatrensis* 2n = 50 (HSU and JOHNSON 1963).

Thus it seems that fossorial rodents fall into two groups that differ from one another in their karyotype characteristics. The one group is typically conservative in its karyotype as though a well adapted arrangement had evolved and been maintained by outbreeding in a sparse, widely-ranging population where ecological conditions were not strikingly varied. *Heterocephalus* is so stereotyped in its adaptations to a dry environment that it has been used as an indicator species for arid conditions (KINGDON 1974). *Heliophobius*, too, lives in low rainfall areas in well-drained soil at low altitudes. *Spalacopus*, however, inhabits both coastal and mountain areas of Chile.

A similar conservatism of karyotype between genera is found in some non-fossorial rodents (MASCARELLO et al. 1974; GEORGE 1979).

The second group of fossorial rodents is typically varied with differing species karyotypes and geographical variation of karyotype within species. Local populations and local species are often isolated and found in different conditions of rainfall and temperature.

It has been suggested that the most important factor in accounting for these two groups of karyotypes is the difference in the social structures of the species. It has been suggested that *Ctenomys, Thomomys, Geomys* and *Spalax* have limited adult vagility, low juvenile dispersal distance and strong territoriality which leads to chromosome diversity (BUSH et al. 1977). But PATTON and YANO (1977), in a detailed analysis of *Thomomys bottae* populations, argued that, in spite of the cytological differences between populations and the territoriality of individuals, considerable gene flow occurs. It occurs mostly over ecologically homogeneous habitats.

Although rather little is known about the social structure of either the octodontids or the bathyergids, REIG (1970) reported that *Spalacopus* is known to be a wandering animal.

The sand puppy *Heterocephalus* lives in extensive burrows of up to about 50 animals and, in some areas, colonies occupy closely adjoining territories (JARVIS and SALE 1971). HILL et al. (1957) reported that colonies can be amalgamated and lone sand puppies assimilated into existing colonies. *Heterocephalus* has a continuous range from Somalia to southern Kenya and is a monotypic genus.

The silver blesmol *Heliophobius* is a solitary animal and little is known about its behaviour except that it is aggressively territorial. In order to find a mate, there must be at least some occasions when adults wander over the surface at night for considerable distances. *Heliophobius* is found extensively over northern Kenya to Rhodesia and, although divided into several species by some authors (ALLEN 1939), KINGDON regards it as one variable species.

Fossorial rodents do not seem to be a group that necessarily has different evolutionary potential from other rodents. It seems more likely that the high diversity that is found in the second category of fossorial rodents is the result of break-up into separate populations as a result of climatic or geomorphological changes in the past (PATTON and YANO 1977) or the result of bottleneck situations (NEI et al. 1975).

The first category may be the result of persistently wide ranging populations in long-established ecological conditions. Species in this category are frequently monotypic, show karyotype conservatism, the retention of old and well tried linkage groups coupled with high chromosome numbers and high recombination indices (high in *Heterocephalus, Spalacopus* and *Thomomys bottae* but low in *Ctenomys*).

In conclusion, it seems dangerous to generalise about fossorial rodents and their karyotypes until more is known of their social and ecological adaptations and their phylogenetic history. Karyotype diversity in contrast to karyotype conservatism may give a better indication of the history of the group than of present social structuring.

Clearly a study of the chromosomes of other species and other populations of bathyergids would be of interest.

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Professor G. M.O. Maloiy of the University of Nairobi kindly gave me the *Heterocephalus* individuals. Dr. S. Gombe, also of the University of Nairobi, organised and took part in the strenuous digging parties for *Heliophobius*. Professor Hyder gave me facilities in the Department of Zoology. I am grateful to them for their help.

Zusammenfassung

Konservativismus der Karyotypen zweier afrikanischer Maulwurfsratten (Rodentia, Bathyergidae)

Es werden die Chromosomen und G-Band-Muster von zwei Gattungen der afrikanischen Nagetierfamilie Bathyergidae untersucht und beschrieben. *Heterocephalus glaber* und *Heliophobius argenteocinereus* haben eine diploide Anzahl von 60 Chromosomen, ähnliche Karyotypen und ähnliche G-Band-Muster. Die Karyotypen werden mit denen von anderen unterirdisch lebenden Nagetieren verglichen. Demnach lassen sich subterran lebende Rodentia in zwei Gruppen unterteilen: in solche mit konservativen Karyotypen (Bathyergidae, Octodontidae) und jene mit variablen Karyotypen (Geomyidae, Spalacidae, Ctenomyidae). Der Unterschied zwischen beiden Gruppen scheint nicht von der Sozialstruktur abhängig zu sein. Deshalb sollte unterirdisch lebenden Nagetieren nicht unbedingt ein anderes evolutives Potential oder eine größere Karyotyp-Variabilität nur aufgrund ihrer subterranen Lebensweise zugesprochen werden als anderen Rodentia.

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